On the Oviposition Habits of 13-Year Versus 17-Year Periodical Cicadas of the Same Species

MONTE LLOYD

DEPARTMENT OF BIOLOGY, UNIVERSITY OF CHICAGO, CHICAGO 60637

AND

JO ANN WHITE

DEPARTMENT OF ZOOLOGY, UNIVERSITY OF NORTH CAROLINA, CHAPEL HILL 27514

RECEIVED FOR PUBLICATION AUGUST 7, 1975

Abstract: Three species of periodical cicadas occur intermixed in roadside vegetation, ovipositing at eye level within easy reach. By collecting these, and noting the plant species on which each individual is ovipositing, one can assess the oviposition preferences of a given species relative to those of other species. The data thus far indicate that both 13-year and 17-year counterparts of *Magicicada septendecula* prefer hickory more than do the other two species, also that both counterparts of *M. septendecim* prefer (more than does *M. cassini*) those tree species that are capable of becoming canopy dominants in mature upland forest.

There are three perfectly synchronized species of periodical cicadas that coexist over most of their range in Eastern North America: *Magicicada septendecim*, *M. cassini*, and *M. septendecula*. They have a 17-year life cycle in the northern part of their range and a 13-year life cycle in the southern part. Alexander and Moore (1962) applied different species names to 13-year cicadas, even though they could find no differences in song, and no differences in morphology between the 13-year and 17-year counterparts for any of the three species. A color difference was claimed between 13- and 17-year *M. septendecim*, but this has never been substantiated or documented quantitatively. In this paper and others to follow, we show that one cannot find any ecological differences between 13-year and 17-year counterparts either. Accordingly, rather than call indistinguishable entities by different species names, we prefer to use the original (17-year) names throughout.

Dybas and Lloyd (1962, 1974, in prep.) have studied the habitat relations of 17-year cicadas in several broods over a period of 18 years. In mature,

Acknowledgments: We are grateful to Henry Dybas (Field Museum of Natural History) and to Charles Strehl for helpful comments, to Floyd Swink and George Ware (Morton Arboretum) for identifying plant specimens, and to B. C. Pass and O. D. Hawkins (University of Kentucky) for permission and assistance in our work at Eden Shale Farm. We thank Dianne and Mike Wonio, Ian and Dylan Lloyd, and the Bioscience 273 class (University of Chicago) for help in collecting ovipositing females at Ramsey Lake. We benefited from comments by referees of a previous version of this manuscript. They made us think and write more clearly. We were supported by grants from the National Science Foundation (GB-38509) and the University of North Carolina Research Council.

closed-canopy forests, *M. cassini* occurs mainly on the floodplain and *M. septendecim* occurs manily on the uplands. The same pattern is found in 13-year cicadas (Lloyd and Dybas, in prep.). *Magicicada septendecula* is usually by far the rarest of the three species. It sometimes occurs in upland patches interspersed with *M. septendecim*, but comes into greatest prominence in forest-prairie ecotone situations, i.e., large open-grown trees (especially hickories) with a grassy understory. We infer that this was the general picture partial separation of periodical cicada species in adjacent habitats throughout the deciduous forests of eastern North America prior to European settlement.

Today, vast areas of former forests are transformed into farmlands and suburban gardens. Woody vegetation persists, e.g., along streams and roadsides, on hilltops or isolated farm plots, on abandoned farms, in public parks, in suburbs. Much of this is second growth, dominated by successional species. Nevertheless, periodical cicadas thrive in this kind of vegetation. Females seem to prefer ovipositing in sunlit vegetation: isolated small trees, open second growth, along forest edges, along roadsides. In such vegetation, the twigs are loaded with cicada eggs to an astonishing degree and the three species often become thoroughly intermixed (White, in prep.). As Alexander and Moore (1962) put it, "—sympatry is about as complete as it possibly could be."

One has all three cicada species ovipositing within easy reach, in the same vegetation, at the same time. This provides an excellent opportunity to investigate oviposition preferences, which may have evolved in former centuries when populations were partially separated in adjacent woodland habitats having different plant species. One simply collects, by hand or by net, females seen in the act of oviposition, and records the plant species on which each is ovipositing. The data fit into a conventional chi-square contingency table analysis. Dybas and Lloyd (1974, Figs 18, 19, Table 11) did this during an emergence of 17-year Brood IV in 1964 at Tall Oaks, near Linwood, Kansas. They found 98/102 *septendecula* females ovipositing in hickory, versus 37/60 for *cassini*, versus 80/286 for *septendecim*, which clearly demonstrates a much stronger preference for hickory in *septendecula* than in *cassini* and *septendecim* (lumping the latter two, Fisher exact test, $P < 10^{-30}$). This result was anticipated from earlier studies of microdistribution (Dybas and Lloyd 1974).

RESULTS AND DISCUSSION

In field studies of other broods, we have often tried to repeat this kind of collection of ovipositing females, but found it difficult because *septendecula* is usually a rare species (Alexander and Moore 1962, Dybas and Lloyd 1974). Table 1 presents the only two cases we have where enough *septendecula* were caught to subject the data to statistical analysis.

The data from 1972 at Ramsey Lake State Park, Illinois, are especially interesting because these are 13-year cicadas (Brood XIX) and hickories are

TABLE 1. Numbers of periodical cicadas laying their eggs in various host species: samples from two different areas and times.

	Ramsey Lake			Eden Shale		
	M. septendecim	*M. cassini*	*M. septendecula*	*M. septendecim*	*M. cassini*	*M. septendecula*
Carya spp. (twigs)	47	11	6	7	21	4
Carya spp. (petioles)	–	3	4	–	2	1
Quercus alba	31	3	–	7	10	–
Quercus stellata	1	–	–	–	–	–
Quercus velutina	20	5	–	8	19	1
Quercus muehlenbergii	–	–	–	4	3	–
Acer saccharum	6	1	–	–	–	–
Ulmus americana	11*	15	1	–	1	–
Ulmus rubra	9	7	–	2	3	–
Fraxinus americana	12	–	2	3	13	–
Cercis canadensis	1	4	–	5	47	5
Juniperus virginiana	1	2	–	–	8	–
Cornus drummondii	6	23	–	–	–	–
Cornus florida	–	–	–	–	1	–
Robinia pseudo-acacia	4	12	–	–	–	–
Gleditsia triacanthos	–	–	–	–	2	–
Crataegus mollis	–	–	–	–	8	–
Crataegus crus-galli	–	–	–	–	1	–
Crataegus pruinosa	19	11	–	–	–	–
Diospyros virginiana	1	–	–	–	–	–
Sassafras albidum	–	–	–	–	5	–
Salix nigra	2	–	–	–	–	–
Prunus serotina	8	15	–	–	–	–
Prunus americana	–	–	–	–	3	–
Totals	179	112	13	36	147	11

Note—At Ramsey Lake State Park, Illinois (13-year Brood XIX, 13–14 June, 1972), the hickories were *Carya laciniosa*, *C. glabra*, and possibly *C. ovalis*, not distinguished. At Eden Shale Farm, near Sweet Owen, Kentucky (17-year Brood XIV, 5–20 June, 1974), the hickories were *Carya ovata* and *C. glabra*, not distinguished.

* One of these may have been in *Ulmus rubra*.

abundant at Ramsey Lake. We anticipate that 13-year *M. septendecula* will prefer to oviposit in hickories, just as 17-year ones do. The prediction is confirmed: 10/13 *septendecula* were caught ovipositing in hickories, versus 61/291 for *cassini* and *septendecim* combined. By Fisher exact test, $P = .00004$.

Also in Table 1 we give data from 1974 at Eden Shale Farm near Sweet Owen, Kentucky (Brood XIV), where hickories were not so abundant as at Ramsey Lake. These data confirm once again the expected preference of 17-year *septendecula* for hickories: 5/11 for *septendecula* versus 30/183 for the other two species. By Fisher exact test, $P = .03$. In our experience thus far, the preference of *septendecula* for hickory is stronger, the more the vegetation itself is dominated by hickory.

Rationale of applying contingency analysis to ovipositing cicadas: It is important to understand what is being tested by the contingency table chi-square (or its equivalent for 2×2 tables, the Fisher exact test), which assumptions are necessary, and which are not. The contingency table does not measure oviposition preference in any absolute sense. To do that, one obviously needs to measure all the twigs of suitable size (3 mm to 11 mm, White 1973) available in an area, and how much of what was available was used by each cicada species. This has been done in another part of Illinois for 13-year Brood XIX in 1972; a full report is in manuscript (White, in prep.). White finds that none of the cicada species oviposits indiscriminantly. Despite the wide variety of plant species acceptable, each cicada species has its own distinct set of preferences.

Based only on a collection of ovipositing females, the contingency table assesses a given cicada species' preferences *relative* to the preferences of other species. Without measuring either, we can still ask whether they were the same, because we know that the availability of the various plant species to the various cicada species was the same. The contingency table is a conditional test. We use it to test the null hypothesis that *septendecula* does not prefer, any more than do the other two species, to oviposit in hickory. We found 10 of 13 *septendecula* females ovipositing in hickory at Ramsey Lake, compared with 61 of 291 females of the other two cicada species. We ask, "What are the chances, under the null hypothesis, of 10 or more *septendecula* ovipositing in hickory?" The answer is $P = .00004$, so we reject the null hypothesis that *septendecula* has no preference for hickory, even though we still have not measured how great that preference is.

Our conclusions obviously apply only to the area that was sampled. We do not know what is happening out of reach in the forest canopy, but this does not affect the validity of our test of the null hypothesis for cicadas at eye level. If we could devise a method to collect ovipositing females in the canopy, we would have a different contingency table with different marginal totals, but test the same null hypothesis. The fact that both cicada and plant species might have different proportions in the canopy versus at eye level makes no difference.

Obviously one must make an honest effort to collect every ovipositing female one sees at eye level, irrespective of what species it is or what plant it is on. If we were deliberately to avoid collecting some individuals of *septendecim* and *cassini* ovipositing in hickory, but assiduously collect all the *septendecula* we saw on hickory, then of course that would invalidate the test. However, non-interactive biases do not do so. *Magicicada septendecula* and *M. cassini* are relatively skittish and harder to catch than *M. septendecim*; we always miss some. *Crataegus* is full of thorns, which makes it harder to collect (by hand or net) all females ovipositing in it. We probably do not catch as high a proportion of females ovipositing in *Crataegus* as there really are. Both kinds of bias affect the marginal totals, but not the validity of the test.

There is a potentially important source of error that is not obvious and is difficult to evaluate. We have what appears to be a homogeneous mixture of three cicada species, but we can't really be sure about it. Males are attracted to the singing of conspecific males (Alexander and Moore 1958) and conspecific females might also be attracted to each other. If so, then they are not moving independently. Such behavior would create a patchy pattern of microdistribution, perhaps unrelated to the patchy pattern of the vegetation. Superimposition of the two would produce a spurious association between cicada species and plant species—an association that would change in different times and places. In other words, a "group" of *septendecula* females might just happen to coincide with a patch of hickory for reasons of historical accident having nothing to do with the properties of hickory, but this would not happen consistently again and again. The statistical contingency test relys absolutely on the unproved assumption that female cicadas choose oviposition sites independently. Perhaps females really do move independently; certainly they move around actively. Nevertheless, to be convincing, this association with hickory (or any other) needs to be demonstrated repeatedly at different times in different places-no matter how great the significance of chi-square for any one time and place. Behavioral studies on female cicadas also need to be conducted.

We hope that further collections of ovipositing females will be made in the next few years.[1] *Magicicada septendecula* is well represented in 13-year Brood XXIII emerging in 1976 in the Mississippi River Valley from southern Illinois to Louisiana. Alexander and Moore (1962) show it also in 17-year Broods XVII, I, and II, emerging in the Appalachians and Eastern Seabord in 1977, 1978, and 1979. Making a large collection of ovipositing females is not difficult, since they do not readily flee when approached. It is merely a matter of being in the right place at the right time.

Analysis for M. cassini versus M. septendecim: So that our conclusions will be statistically independent of those for *M. septendecula*, we omit that species in what follows. From the work of Dybas and Lloyd (1962, 1974), one can anticipate that *septendecim* should prefer upland forest species more than *cassini*, which should prefer floodplain species more than *septendecim*. If the collection site contains an adequate representation of plant species, the hypothesis should be testable. Notice in Table 1 that no floodplain species of hickory, oak, or maple are represented—all are upland species. If we consider ashes and elms as floodplain species, then the hosts can be grouped as follows: (hickories, oaks, and sugar maple) vs (ashes and elms) vs (others). By our *a priori*

[1] If any readers wish to make their own collections of ovipositing females, separated according to plants being used, the authors will be delighted to help with identifying the cicadas. We will also be pleased to have your pressed plant specimens competently identified.

hypothesis, neither cicada species should show any relative preference for "others".

We begin with the Eden Shale data for 17-year cicadas. Using the above lumped categories for host species (listed in the same order), the expected numbers of ovipositing *M. septendecim* females, on the null hypothesis of no preference, were (16) vs (4) vs (16)—rounded to the nearest integer. Observed were (26) vs (5) vs (5). Conversely, for *M. cassini*, we expect (65) vs (17) vs (64) and observe (55) vs (17) vs (80). From this 2×3 contingency table, chi-square is 17.2, $P < .0002$. The deviations from expectation are statistically significant, but somewhat contrary to the predicted pattern. *M. septendecim* shows a relative preference for upland species as predicted, but *cassini,* instead of showing a relative preference for floodplain species, is relatively prone to oviposit in "others". These "others" are mainly shade-intolerant, successional, second-growth species (mainly redbud, red cedar, hawthorn, and sassafras) that will readily invade cleared land anywhere, whether in upland or floodplain topographic situations. None of these species are dominant canopy trees in virgin forests; all have doubtless increased greatly in abundance following European settlement.

On reflection, this pattern of *cassini* ovipositing in "others" is understandable and might have been anticipated. Except for forested mountainous regions in the Eastern United States, vast areas of original forest have been cleared for farmland (see Dybas and Lloyd 1974 for an account of Ohio). Floodplain forests have been cleared sooner and more thoroughly than upland forests because alluvial soil is generally more fertile and easier to farm than is the adjacent upland soil. In Oklahoma, owing to suppression of fires, upland forests have actually increased since European settlement—but not floodplain forests (Rice and Penfound 1959). For both *M. septendecim* and *M. cassini*, it has been advantageous to oviposit in the enormously expanded acreages of second-growth woody species: the young sunlit trees are rapidly growing, root/shoot ratios are high (Lyr et al. 1963), and prospects for survival of the nymphs are good. But for *cassini*, in addition, it has often been disastrous to oviposit "as usual" in the ashes, elms, hackberries, and sycamores of floodplain forests when, over the next 17 or 13 years, these forests have been converted into cornfields or the remnants of floodplain forest permanently flooded by dams.

Two possible hypotheses come to mind. The first would be statling if true: (1) Originally *M. cassini* may have had some inherited behavioral pattern that led it to prefer ovipositing in the tree species characteristic of floodplain forests, just as *M. septendecim* now demonstrably prefers to oviposit in upland species. However, during the 150 years or so since European settlement (about 9 or 12 cicada generations), the relatively greater destruction of floodplain than of upland forests has exerted relatively greater selective pressures on *cassini*, and this has brought about genetic changes affecting its oviposition behavior. That would be rapid evolution indeed.

An alternative hypothesis assumes no genetic changes and is testable: (2) Adult cicadas prefer to oviposit in the twigs of the same plant species on whose roots they fed as nymphs. Most ovipositing females of *septendecim* immigrating to recent second growth (less than 17 or 13 year old) have probably come from the large oaks, hickories, and maples of nearby upland forests, whereas most immigrating *cassini* females have probably come from older second growth, since mature floodplain forests are so scarce. If the females simply tend to stick with whatever they grew up on, this would explain how a population of *cassini* could change its oviposition habits (assuming that they did) so rapidly. This second hypothesis would also explain why the preference of *septendecula* for hickory appears to be stronger where the vegetation is more dominated by hickory, as we mentioned earlier. We plan to test this idea directly with field experiments.

We next ask whether the same pattern is exhibited in our sample of 13-year cicadas (Brood XIX) from Ramsey Lake. Here the second-growth species are mainly roughleaf dogwood, black locust, frosted hawthorn, and black cherry (Table 1). On the null hypothesis of no preference, the contingency-table expected numbers of ovipositing *septendecim* are (79) vs (33) vs (67). Observed were (105) vs (32) vs (42). For *cassini*, we expect (49) vs (21) vs (42) and find (23) vs (22) vs (67). The deviations are highly significant statistically (chi-square is 47.2, $P < 10^{-10}$), and in exactly the same direction as seen with 17-year cicadas. On present evidence, it appears that differences in oviposition preferences between *Magicicada septendecim* and *M. cassini* are the same differences, whether they are 17-year or 13-year cicadas.

To summarize, three hypotheses were anticipated by previous experience and have been corroborated by the data on oviposition available so far: (1) *Magicicada septendecula* prefers hickory more than the other two species do, (2) *M. septendecim* prefers upland forest species more than *M. cassini* does, and (3) there are no differences between 13-year and 17-year cicadas of the same species.

Evidence is accumulating to support the idea that 13-year periodical cicadas evolved from 17-year ones by the same process—4-year accelerations—that gave rise to a succession of 17-year broods 4 years apart (Lloyd and Dybas 1966, White and Lloyd 1975). It appears that 4-year accelerations are still occasionally taking place (Lloyd and White in press, Lloyd and Dybas in prep.). The entire evolutionary process, including the generation of 13-year broods, may have occurred quite recently, possibly since the last glaciation, and may still be going on. If this were so, then it would come as no surprise if

13- and 17-year cicadas of the same species had not evolved ecological differences.

Literature Cited

Alexander, R. D., and T. E. Moore. 1958. Studies on the acoustical behavior of seventeen-year cicadas (Homoptera: Cicadidae: *Magicicada*). Ohio J. Sci. **58:** 107–127.

——— and ———. 1962. The evolutionary relationships of 17-year and 13-year cicadas, and three new species (Homoptera, Cicadidae, *Magicicada*). Misc. Publ. Mus. Zool., Univ. Mich. **121:** 1–59.

Dybas, H. S., and M. Lloyd. 1962. Isolation by habitat in two synchronized species of periodical cicadas (Homoptera: Cicadidae: *Magicicada*). Ecology **43:** 444–459.

——— and ———. 1974. The habitats of 17-year periodical cicadas. (Homoptera: Cicadidae: *Magicicada* spp.). Ecol. Monogr. **44:** 279–324.

Lloyd, M., and H. S. Dybas. 1966. The periodical cicada problem. I. Population ecology. Evolution **20:** 133–149. II. Evolution. Ibid. 466–505.

——— and J. White. (in press) Sympatry of periodical cicada broods and the hypothetical 4-year acceleration. Evolution.

Lyr, v. H., G. Hoffmann, and K. Dohse. 1963. Über den Einfluss unterschiedlicher Beschattung auf die Stoffproduktion von Jungpflanzen einiger Waldbäume. I. Mitteilung. Flora, Jena **153:** 291–311.

———, ———, and W. Engel. 1963. ———. II. Mitteilung. Flora, Jena **155:** 305–330.

Rice, E. L., and W. T. Penfound. 1959. The upland forests of Oklahoma. Ecology **40:** 593–608.

White, J. 1973. Viable hybrid young from crossmated periodical cicadas. Ecology **54:** 573–580.

——— and M. Lloyd. 1975. Growth rates of 17- and 13-year periodical cicadas. Amer. Midl. Nat. **94:** 127–143.

BOOK REVIEW

Ecological Animal Parasitology. C. R. Kennedy. 163 pp. Halsted Press; John Wiley & Sons, New York. $11.95. 1975.

This is a very concise introduction to the ecology of animal parasites. The book is extremely readable, authoritative, and accurate. The list of references is not very extensive (less than 200), referring to many reviews in which the original references are cited. This practice makes it more difficult and time consuming to find the relevant papers but otherwise detracts little from the value of this book. The volume can be recommended to both undergraduate and graduate students first encountering the problems of parasitology and tropical medicine. The topics discussed are timely and will appeal to experts as well as to newcomers in parasitology.

Karl Maramorosch
Waksman Institute of Microbiology, Rutgers University